The accumulation of species and recovery of species composition along a 70 year successional gradient in a tropical secondary forest

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Abstract

The majority of global forests are secondary and are at different stages of succession. Assessing the dynamics of species richness and similarity, and quantifying the importance of environmental filtering, dispersal limitation and other stochastic processes are essential to understanding the mechanisms of succession for forest restoration. In this article, we explored the accumulation of species, the relative importance of spatial distance, environmental factors and stand age in determining species composition of a tropical secondary forest succession in Hong Kong. Twenty-eight plots with median age of 7, 20, 39, 61 and over 70 years in the secondary forest were established and surveyed, and the indicator species for each age class were identified. Species composition shows large variation both within and between age classes, while species richness in the old growth forest (>70yr) was significantly lower than in the mid-age classes. Rarefied species richness showed a rapid accumulation during early succession, but species richness levelled off from 20 yrs onwards. Variation partitioning indicated that spatial distance alone explained 33% of the variation in species composition, followed by environmental distance (8%) and stand age (1%). The results of Nonmetric Multidimensional Scaling suggested that idiosyncratic successional pathways and alternative stable states might be prevalent. Our results suggested dispersal limitation was the main limiting factor in explaining the turnover of species during forest succession, while environmental filtering played a lesser role in shaping species distributions. Our results highlight the importance of active restoration in overcoming the barriers of succession in secondary vegetation in the tropics.

Key Words: subtropical, degraded landscape, secondary forest, dispersal limitation, environmental filtering, species assembly, priority effect, successional pathways

1. Introduction

According to recent studies, 82% of the world's remaining forests have been degraded or fragmented by human activities (Chazdon, 2008; Collins et al., 2017; Holl, 2017; Watson et al., 2018), which have not only altered the forests' species composition, but also their structure and ecological functions (Ibanez et al., 2017; Måren et al., 2018; Purschke et al., 2017). Understanding the dynamics and the mechanisms behind forest recovery is vital for their conservation and restoration of biodiversity (Arroyo-Rodríguez et al., 2017).

Factors including environmental filtering, dispersal mechanism, spatial patterns and processes and soil nutrient availability, which affect species composition and the speed of succession, play important roles in governing the species assembly. These factors are classified into niche-based processes (according to the niche-based theory, (Tilman, 2004)) and stochastic processes (according to neutral theory, (Hubbell, 2005)) based on the underlying mechanisms controlling the species assemblage processes along successional gradients. Niche-based theory is best explained by environmental filtering whereby only species with certain functional traits are able to colonise and recruit in a habitat (Kraft et al., 2015; Lebrija-Trejos et al., 2010b), whereas the neutral theory assumes that the occurrence of species follows completely random patterns, eg. dispersal, speciation, local extinction *etc*, and has been successful in explaining a number of biodiversity patterns (Leibold and McPeek, 2006; Volkov et al., 2003). It is now widely accepted that both processes play important roles in determining community assembly (Lebrija-Trejos et al., 2010a).

Another approach to understanding the mechanisms regulating species composition along the successional gradient is to analyze the convergence or divergence of species,

which could also provide insight into the speed and direction of succession (Norden et al., 2011). For example, in a relatively homogeneous environment, habitat filtering should lead to the convergence of species composition, whereas stochastic processes should lead to the divergence of species composition. However, these processes become complicated by the increase in habitat heterogeneity and the degree of habitat degradation (Lebrija-Trejos et al., 2010a). Therefore, how the underlying factors interact with each other causing a convergence or divergence of species compositions along a successional gradient remain uncertain, as their relative importance changes over time (Måren et al., 2018).

At the early stage of secondary succession, a degraded habitat leads to a more open and drier habitat, imposing higher environmental filtering effects on the colonising species, resulting in the convergence of species composition. The more degraded a site, the more environmental filtering occurs (Purschke et al., 2013). At the stand initiation stage, large degraded areas together with harsh and exposed site conditions limit the number of suitable species to recruit from the remaining species pool (Purschke et al., 2013), and lead to the convergence and stability in species (Arroyo-Rodríguez et al., 2017; Williamson et al., 2014). In many tropical areas, grassland develops as a final, stable but alternate degraded stage after the complete removal of rainforest (Aide and Cavelier, 1994). On the other hand, at later successional stages, the recruitment of shade-tolerant trees and understory species depends entirely on the improvement of environmental conditions by progressing succession and species' availability in the active species pool (de Bello et al., 2012; Kirmer et al., 2008).

One way to characterize the community structure is analyzing the indicator species (Dufrene and Legendre, 1997), specifically, the Dufrene-Legendre Indicator Species Analysis, in which a species' indicator value is the product of its relative frequency and the

74 average abundance in the cluster (Roberts, 2016). The indicator value of a species within a
75 certain habitat shows its fidelity and specificity to the habitat (McGeoch et al., 2002). The
76 indicator species, however, can not only be used to characterize different vegetation types,
77 or habitat, but can also insights for different age classes to show how communities change
78 over time.

79 Theoretically, the smaller the species pool, the more likely species composition would
80 converge (Lebrija-Trejos et al., 2010a). The available species pool in a degraded landscape
81 is highly linked to the degree of degradation and fragmentation of the habitat, which often
82 cause local extinctions (Matthies et al., 2004). Often in highly degraded areas, only a
83 fraction of species are able to survive and to re-colonise, compared to the intact active
84 species pool of a primary forest (Lavergne et al., 2005).

85 Thus the degree of disturbance has a huge impact on forest succession, and recovering
86 secondary forests under different disturbance regimes may have contrasting diversity
87 patterns and successional pathways (Cole et al., 2014). For example, in clear-cut or
88 selectively logged forest in Hainan island half a century of recovery was sufficient to
89 restore a species richness and biomass similar to a primary forest, but the species
90 composition and community structure were very different (Lu et al., 2016; Xu et al., 2015).
91 On the other hand, comparatively small canopy gaps in primary forest caused by natural
92 disturbance appear able recover to their original state within just 141 years (Yang et al.,
93 2017).

94 Hong Kong is now one of the rare examples where tropical secondary forest is
95 regenerating naturally on land abandoned after agricultural use and/or deforestation. A
96 diverse tropical seasonal rain forest was the primeval vegetation of Hong Kong (Xing et al.,
97 1999), but most was cleared thousands of years ago for farming (Zhu, 2017). Nonetheless,

Hong Kong's present day flora and fauna represent recovery since 1945 due to both natural regeneration from tiny remnants in inaccessible sites and possibly from the post-war (World War II) plantation of a limited range of native and exotic species. Succession in these secondary forests is frequently disturbed by fire induced by local residents (Abbas et al., 2016). However, the successional pathway and rate of recovery of the secondary forest to fully functional and diverse forest remain unknown.

In this study, the structural changes associated with this forest recovery over the past 70 years are documented and mapped by sequential analysis of aerial photographs and satellite images. Thus it is possible to record and study changes in species composition along the successional and environmental gradients and thereby understand the process of ecosystem recovery in the degraded tropical landscape of Hong Kong. We used data collected from 28 plots in the tropical secondary forest with different stand ages to address the following questions: (i) Are species richness, stem density, growth form and indicator species significantly different in the different successional stages? (ii) Does species similarity converge or diverge along the 70 year successional gradient? (iii) Which are the factors influencing species composition and turnover?

2. Materials and Methods

2.1. Site Description

Hong Kong is located east of the Pearl River estuary in south China at 22º09'-23º37' N and 113º52'-114º30' E (Fig. 1a), with a land area of 1106 km^2. The climate is seasonal, with a hot humid summer and a cool dry winter. Annual rainfall ranges from 1800-3100mm of which 80 % occurs between May and September. Mean annual temperature is 22-23°C with minima and maxima in January and July, respectively. Hong Kong's original vegetation was diverse seasonal and evergreen rain forest, with 150-180 woody species per hectare, as found in nearby protected areas in south China (Fang et al., 2004; Xu et al.,

2015). However, because of intense human disturbances, current woody vegetation only comprises secondary forest, plantations and Feng Shui Woods (Zhuang and Corlett, 1997). The majority of the present secondary forest has developed through succession since 1945.

The study area covers Tai Mo Shan and Shing Mun Country Parks in the New Territories of Hong Kong (Fig. 1). The topography is rugged, characterized by convex slopes rising to the highest mountain Tai Mo Shan (957 m) and steep slopes around the Shing Mun Reservoir. Previous analysis of the sequential habitat maps showed that the landscape had transformed from a grassland dominated, to a forest dominated landscape over 70 years of succession. Forest cover increased over time from 0.17 % of the landscape in 1945 to 36.50 % in 2014 (Abbas et al., 2016).

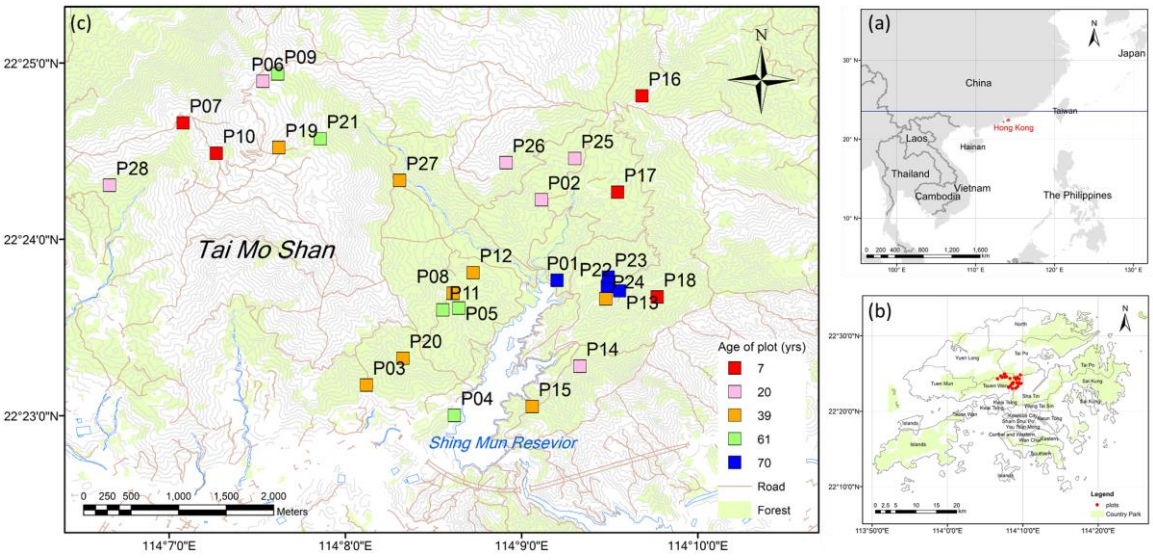

Figure 1 Location of the study area and the plots: a. Location of Hong Kong; b. Location of Tai Mo Shan and the 28 plots; c. Location of the 28 plots and the age of succession.

2.2. Plot data collection

We used three sets of aerial photographs of 1945 (scale -1:40,000), 1963 (scale – 14,000) and 1989 (scale -1:20,000), and two satellite images of 2001 (spatial resolution – 1 m) and 2014 (spatial resolution – 0.5 m) to map structural forest succession over the last 70

140 years (Abbas et al., 2016). The age of each plot was estimated based on sequential analysis
141 of vegetation cover. For example, if a plot was not covered by woody vegetation in year T_1,
142 but was covered in year T_2, the age of the plot was estimated as the mid-point between
143 years T_1 and T_2. All plots were grouped into five age categories; 7, 20, 39, 61 and 70yrs
144 defined by the time since recovery, (0-14], (14-26], (26-52], (52-70] and >70yrs,
145 respectively. All plots >70 yrs were Feng Shui Woods in Shing Mun Country Park and
146 should be at least 100-150 years old (Fig 1c).

147 Considering the heterogeneity of the landscape and accessibility, it was difficult to find
148 representative stands through random selection, therefore, a stratified random sampling
149 method was used to select plot locations. All the plots were grouped into the five age
150 categories defined by time since recovery (Fig. 1b). Plots were set up at an altitudinal
151 interval of 200m, with further considerations for aspect (N, NE, E, SE, S, SW, W and NW),
152 and slope (flat, gentle, moderate and steep), whenever possible. In total, the plots occupy
153 1.12 hectares (Fig 1c, Table 1) at elevations ranging from 205m to 822m.

154 *Table 1. Number of plots under each age class*

Age of succession	Number of plots	Age midpoint
(0-14]	5	7
(14 – 26]	6	20
(26 – 52]	8	39
(52-70]	5	61
>70	4	70

155 Field survey was conducted between March 2015 and May 2016. All trees with
156 diameter at breast height (DBH) ≥ 1cm were tagged, identified, measured and located in the
157 plot. The names of plant species were standardized following The Plant List (Version 1.1,
158 http://www.theplantlist.org/) using the R package plantlist 0.3.7 (Zhang, 2018). Only
159 woody plant species were recorded and identified. We classified the species into four

growth forms based on the *Flora of Hong Kong* (http://www.herbarium.gov.hk) and field experience: (1) canopy tree; (2) small tree; (3) shrub and (4) scandent shrub or liana, and their proportion in each successional stage were analysed.

2.2.1. Environmental Factors

Topographic variables used in the present study include elevation, slope, curvature and aspect. Elevation was extracted from a 2m resolution Digital Elevation Model (DEM), and slope, aspect and curvature were calculated using SAGA software (Conrad et al., 2015). Soil samples were collected in May to June 2016, for measurement of texture (sand, silt or clay), pH, organic matter, carbon content, nitrogen content and moisture. Each soil sample was collected from the center of the 20m x 20m plot at a depth of 20 cm after the surface litter was removed.

2.3. Data analysis

2.3.1. Species Richness and Indicator Species for Different Age Classes

Species richness tends to vary with sampling intensity and stem density. To compare species richness between different age classes, we used rarefaction to control the difference in stem density among sites that may arise due to stage of succession as well as edaphic and topographical factors. Rarefaction was performed using function rarefy() in 'vegan' 2.5-1 (Oksanen et al., 2018). We randomly sampled 107 individuals from all the 28 plots to estimate species richness. Indicator species of each age class were determined using Dufrene-Legendre indicator analysis (Dufrêne and Legendre, 1997) in the R package labdsv 1.8-0 (Roberts, 2016).

2.3.2. Testing the Dissimilarities of Plots in Species Composition

To quantify the species dissimilarities between each pair of plots, Jaccard, Morisita, Horn-Morisita, Bray-Curtis and Chao dissimilarities were employed. Jaccard dissimilarity is incidence based, in which the occurrence of species is treated as presence-absence, and it only represents the change in species composition (Oksanen et al., 2018). Morisita, Horn-Morisita and Bray-Curtis dissimilarities take abundance into account, and thus can reflect changes in species composition as well as abundance. The Horn-Morisita index weights abundant species more heavily than rare species, while the Morisita index only takes abundance into account (Jost et al., 2011). Chao dissimilarities consider the species missing from the species pool (Chao *et al.* 2005). All the dissimilarities were computed using vegdist() in vegan (Oksanen et al., 2018).

We explored the relationships between dissimilarities with spatial distance, topographic variables, soil properties and age using Mantel's test (Mantel, 1967). To make all the variables comparable, the topographic variables and soil properties were subtracted from the mean of each variable and divided by its standard deviation. All the explanatory variables were then converted to a distance matrix and the correlations between Jaccard, Morisita, Horn-Morisita, Bray-Curtis and Chao dissimilarities, and the topographic, soil, spatial and age distances were explored. P values were assessed based on 9999 random permutations.

We used Nonmetric Multidimensional Scaling (NMDS) to show how dissimilarity changed within and between each age class. NMDS analysis was carried out using metaMDS() in vegan. The Multi Response Permutation Procedure and Mean Dissimilarity Matrix (MRPP) algorithm was employed to ascertain if the mean distance within each group was significantly different from the mean distance of all the plots based on 9999 permutations. To quantify the homogeneity of dissimilarity variances within each age class, the variances of dissimilarities were compared using betadisper (Anderson, 2006). This test

is analogous to Levene's test for homogeneity of variances. Finally, we used analysis of similarities (ANOSIM) to test if there was a significant difference between age classes (Clarke, 1993; Warton et al., 2012). The P-value was also obtained based on 9999 permutations.

We used variation partitioning to quantify the relative importance of environment (Legendre et al., 2009), spatial distance and age in determining the species composition. The spatial distance matrix between the 28 plots was converted to the Principal Coordinates of Neighborhood Matrix (PCNM) (Borcard and Legendre, 2002). PCNM vectors which were significantly correlated with species composition were selected using both forward and backward selection based on RDA (redundancy analysis). Only the vectors with $P<0.05$ were used in the subsequent analysis. Principal Component Analysis (PCA) was applied to the environmental variables (topographic and soil variables) and the significant components were selected by RDA, in which the limits of permutation P-values for adding or dropping a term to/from the model was 0.05. These analyses identified three PCNM vectors (1st, 2nd and 7th) and two environmental components that significantly affect the species composition. All the analyses were conducted in R 3.5.0 (R Core Team, 2018).

3. Results

A total of 8575 individuals of DBH ≥ 1cm woody species belonging to 229 species and 63 families were measured, identified and recorded (SI Table 1). The number of individuals within a plot ranged from 107 to 511, with the mean of 292.8 (density: 7320/ha). Two species from *Symplocos*, *Machilus* were identified to genus level, and one species from Lauraceae was identified to family level. Three gymnosperm species were recorded, including: *Cunninghamia lanceolata*, *Gnetum luofuense* and *Pinus elliottii*. Six exotic and invasive species were recorded: *Acacia confusa*, *Duranta erecta*, *Eucalyptus exserta*, *Lantana camara*, *Lophostemon confertus* and *Pinus elliottii*. In addition, *Cunninghamia*

lanceolata and *Dimocarpus longan*, two species, which are native to Central and south China respectively but also have a long history of cultivation in the region, were recorded.

Species accumulated rapidly during the first 20 years (Fig. 2b). The number of species leveled off from the first 20 years onwards, and declined in the plots above 70 years of age (Fig. 2b). One-Way ANOVA showed that species richness did not differ between different age classes for both species richness ($F_{1, 26} = 0.535$, $P = 0.471$) and the rarified species richness ($F_{1, 26} = 0.206$, $P = 0.653$). Differences in number of individuals (density) could not be detected by one-way ANOVA ($F_{4,23} = 1.623$, $P = 0.202$) although the median for the 7 yrs old plots is 170/400m^2 (4250/ha), while for other age classes median values ranged from 201 to 328/400m^2 (8200/ha).

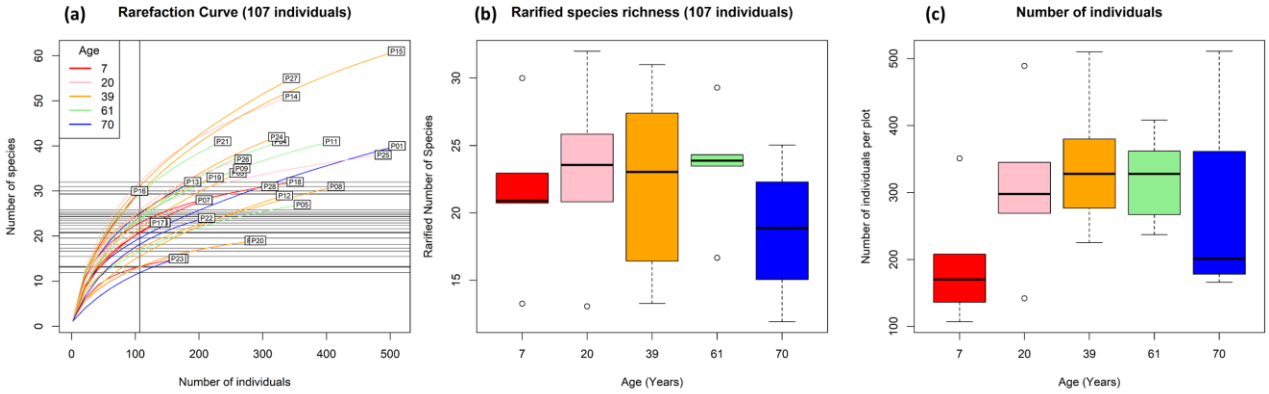

Figure 2: Species richness and density of individuals of different age classes: a. Species rarefaction curve with labels showing plot ID. Note that Plot 16 only had 107 individuals therefore the species richness for each plot was rarified based on 107 individuals; b. Boxplot showing the rarefied number of species in each plot of different successional age classes; c. Boxplot showing the number of individuals within each plot of different successional age classes.

The number of canopy tree species increased from 24.5% (of the total number of observed species) in the first 20 years to 50% in old growth forest. Meanwhile, the proportion of shrub species declined from 41.83% to 20.6%. The proportion of small trees was relatively stable along the successional gradient, ranging from 23.5 to 30.3% (Fig. 3 a), but proportion of scandent shrub or liana species fell remarkably from 10.2% (20yrs) to

2.94% (>70yrs). The number of individuals of canopy tree species increased from 21.96% (39yrs) to 53.5 % (>70yrs) (Fig. 3 b). The proportion of shrub species fell from 57.0% (39yrs) to 24.7% (>70yrs), although the highest proportion of shrub species was observed in the mid-age classes (20-61yrs). Likewise, the highest proportion of scandent shrubs or lianas also occurred during the mid-age classes (3.1% at 61yrs), with both early successional (0.8% at 7yrs) and old-growth forest (0.93% at >70yrs) being less than one percent. In contrast, the proportion of small trees did not show a large difference between different age classes (from 19.3% ~ 26.5%).

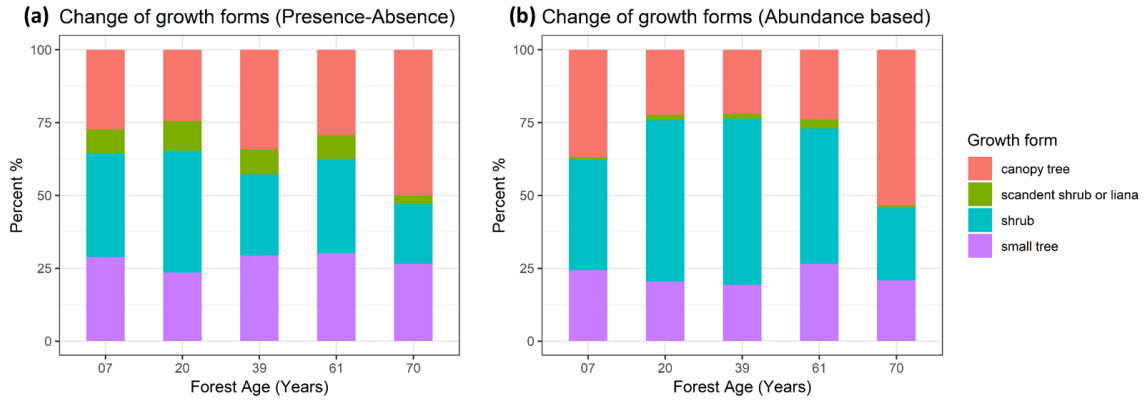

Figure 3. The proportion of different growth forms among different age classes based on: a. Number of species; b. Number of individuals.

Indicator analysis (Fig. 4) revealed that plots at the early stage of succession (7yrs) were characterized by *Machilus chekiangensis*, *Melastoma malabathricum* and *Melicope pteleifolia*, and old plots over 70 years were characterized by *Bischofia javanica*, *Bridelia balansae*, *Choerospondias axillaris*, *Cryptocarya chinensis*, *Elaeagnus loureiroi*, *Elaoecarpus chinensis*, *Elaoecarpus dubius*, *Machilus chinensis* and *Sarcosperma laurinum*. For plots of the next youngest age class (14-26 years old) *Diplospora dubia* and *Wikstroemia nutans* were identified as indicator species, and for plots of medium age, 52-70 years old, *Glochidion eriocarpum*, *Maesa perlaria* and *Osmanthus matsumuranus* were identified as indicator species. However, the indicator values of the medium age class were

much lower than those from other age classes (Fig. 4). Indicator analysis did not identify any species with high indicator value for plots between 20 to 61 years, except for *Diplospara dubia* and *Wikstroemia nutans*. Not all common and abundant species were identified as indicator species, for example: *Psychotria asiatica* and *Aporosa octandra*. Meanwhile, species occurring in few plots, but in high densities were also not identified as indicator species. For example, *Memecylon ligustrifolium* (104 individuals) only occurred within plots > 70yrs, and while 151 individuals of *Lasianthus chinensis* were found in one plot > 70yrs, only 1-5 individuals were found from plots of other age classes (SI Table 4).

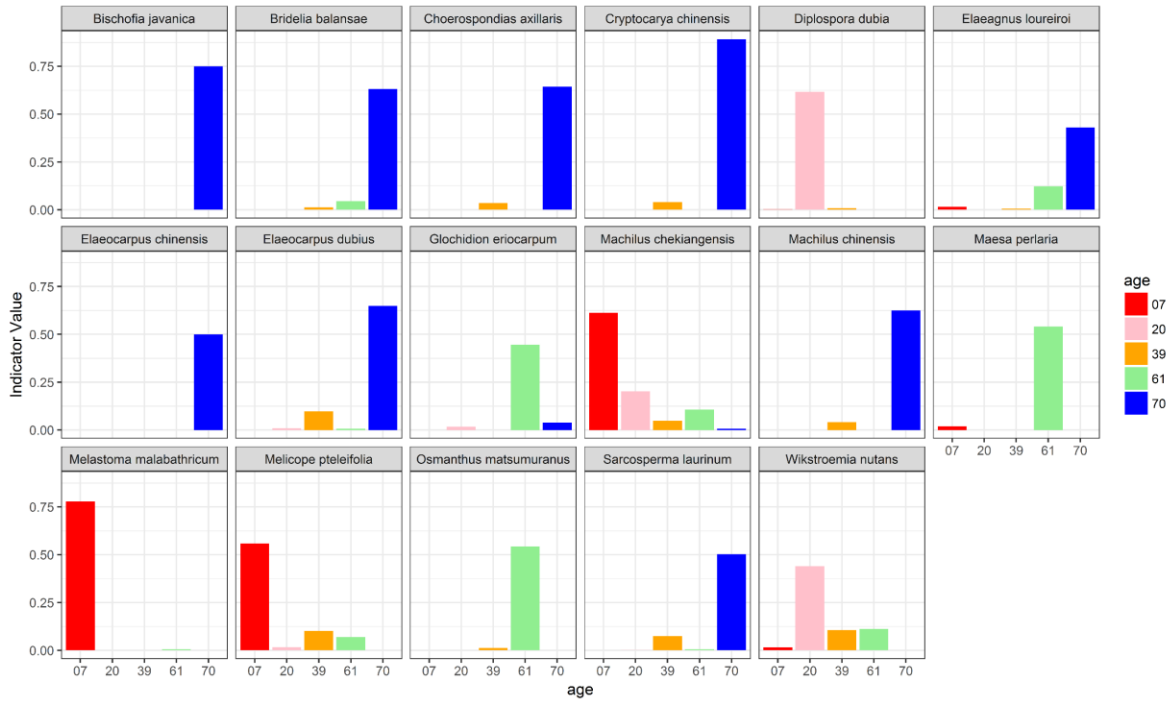

Figure 4. The indicator species for each age class as determined by the Dufrene-Legendre Indicator Species Analysis

Mantel's tests showed a strong influence of spatial distance on Jaccard dissimilarity (Mantel's r = 0.4777, P = 1.00E-04) followed by age (Mantel's r = 0.2644, P < 6e-04) (Table 2). Surprisingly, topographic factors were less related (Mantel's r = 0.2582, P = 0.0042) to Jaccard dissimilarities compared to spatial distance. When topographic variation and soil properties were combined as environmental variables, the correlation became

closer (r = 0.3053, P = 0.0012). This pattern was further supported by Mantel's test on Morisita, Horn-Morisita, Bray-Curtis and Chao dissimilarities in which spatial distance was always the most closely related variable to species dissimilarity (Table 2).

Table 2 Mantel test of pairwise correlation between distance matrices of species dissimilarities and environmental factors (significance is based on 9999 permutations)

	Spatial		Topographic		Soil		Age	
	r	p-value	r	p-value	r	p-value	r	p-value
Jaccard	0.4777	1.00E-04	0.2582	0.0036	0.2318	0.0114	0.2644	0.0010
Morisita	0.4840	1.00E-04	0.2650	0.0061	0.2216	0.0230	0.2553	0.0020
Horn-Morisita	0.4835	1.00E-04	0.2643	0.0061	0.2237	0.0226	0.2558	0.0014
Bray-Curtis	0.4906	1.00E-04	0.2776	0.0033	0.2150	0.0221	0.2739	3.00E-04
Chao	0.4792	1.00E-04	0.3596	2.00E-04	0.1182	0.1380	0.2124	0.0026

The result of NMDS based on Jaccard dissimilarity showed that species composition could be very dissimilar within an age category (Fig. 5 a). The plots within the 7 yrs category were slightly clustered, while at least two plots (plots 17 and 18) were very similar to the 20-61 year-old plots (Fig. 5 a-b). Plots over 70yrs formed a cluster in which only plot P13 was more similar to the plots from other age categories. Plots of 20, 39 and 61 years were distributed around the center of the NMDS plots, and the ordination ellipses (showing 60% confidence interval as computed by stat_ellipse in ggplot2 (Wickham, 2016) overlapped with each other, showing that mid-aged plots shared a similar species pool (Fig. 5a). Plots from different age classes could be either very similar or very dissimilar, depending on the recruitment of species. Surprisingly, by taking abundance into account (Bray-Curtis distance), the overall similarity between plots from 70yrs and 7yrs may be even closer, compared to other age classes, probably due to the lower density of individuals (Fig. 2 c). Plots of 20, 39 and 61yrs were still blended, and the ordination ellipses for each age class were as largely overlapping (Fig. 5, a, b). The NMDS for Chao, Horn-Morisita, and Morisita dissimilarities all showed, that plots >70yrs were distinct from the other age classes while plots from the category 7yrs may be in a distinct cluster (supporting

information SI Fig. 2 a-c). Therefore, the species composition of the mid-aged plots does not converge to the later successional stage of plots >70yrs.

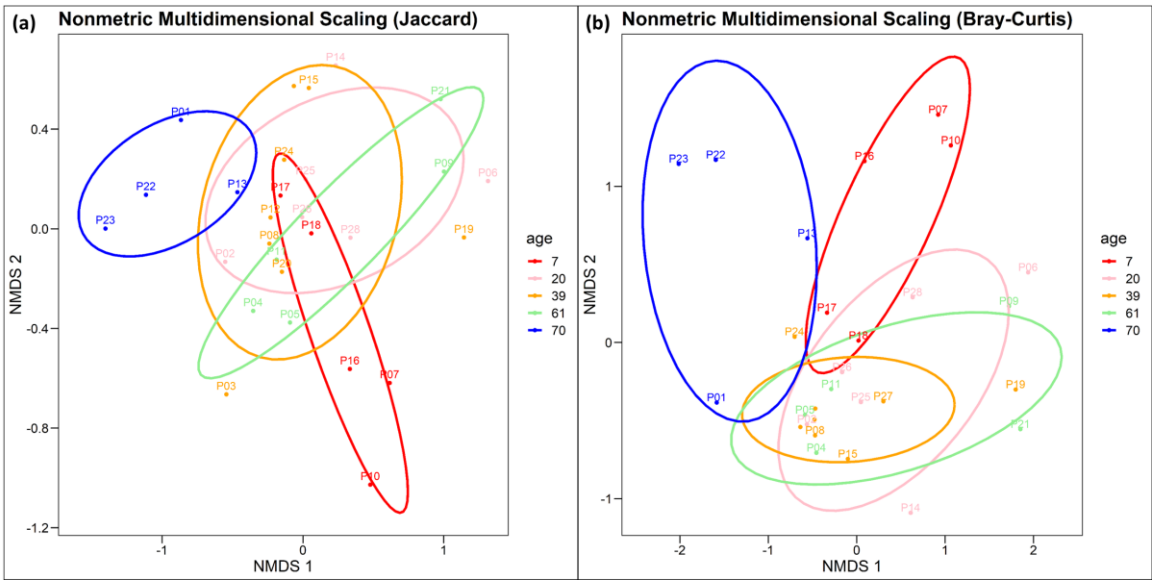

Figure 5: a. Nonmetric Multidimensional Scaling (NMDS) analysis based on Jaccard dissimilarity. b. NMDS based on Bray-Curtis dissimilarity. Ellipses showing 60% confidence interval for each age class.

Analysis of homogeneity (betadisper) for each group showed that the species composition within each age class still varied along the successional gradient, as evidenced by the mean distance to the centroid of each group (Fig. 6a, b). The dispersion of the variance of dissimilarities along the successional gradient showed that the differences were not significant among all the age classes for abundance-weighted dissimilarities (Jaccard dissimilarity, $F_{4,23}$ = 0.2762, P = 0.8903; Morisita dissimilarity: $F_{4,23}$=0.6789, P = 0.613; Horn-Morisita dissimilarity: $F_{4,23}$ =0.6892, P =0.6069; Bray-Curtis dissimilarity: $F_{4,23}$ = 0.4611, P = 0.7635; Chao dissimilarity: $F_{4,23}$=0.4198, P = 0.7926). Analysis of similarity (ANOSIM) revealed that the species composition was significantly different (Jaccard dissimilarity: ANOSIM statistic R: 0.2107, P = 0.0053; Horn-Morisita dissimilarity: ANOSIM statistic R: 0.261, P = 0.0026; Bray-Curtis dissimilarity: R = 0.3131, P = 5e-04; Chao dissimilarity: R

= 0.2167, *P* = 0.0047) between age classes. Additionally, results of MRPP showed that the species composition from plots >70yrs tended to be dissimilar to that from other age classes (SI Fig. 1, a-d).

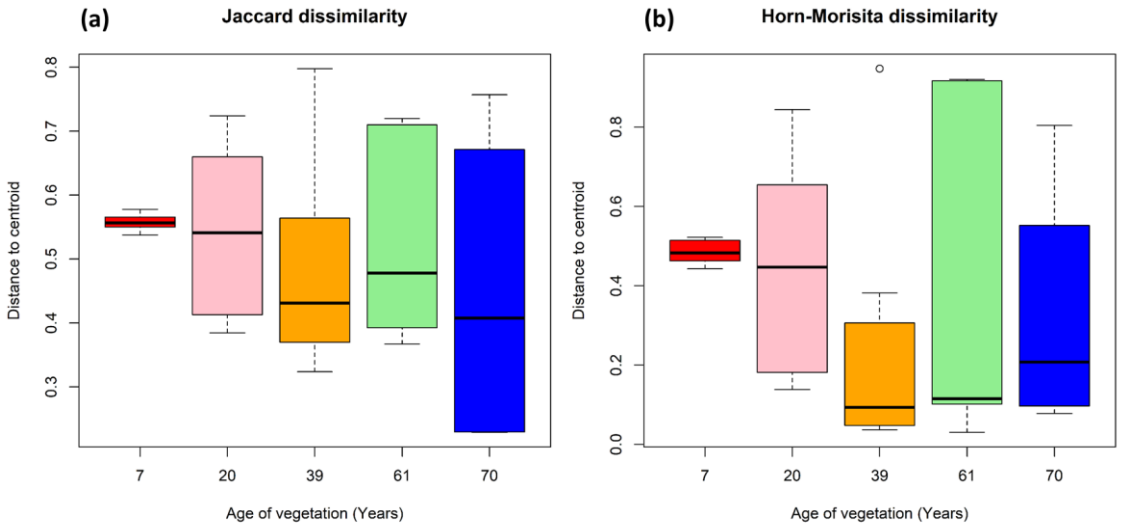

Figure 6. Mean distance to the centroid of each age class based on a. Jaccard dissimilarity; b. Horn-Morisita dissimilarity.

Furthermore, variation partitioning revealed that spatial distance alone explained 33% of the total variation in species composition, whereas environmental variables explained 8% of the variance. In comparison, stand age only explained 1% of the species composition. In total, spatial distance, environmental factors and stand age together explain 50%, leaving the other 50% of variations in species composition unexplained (Fig. 7).

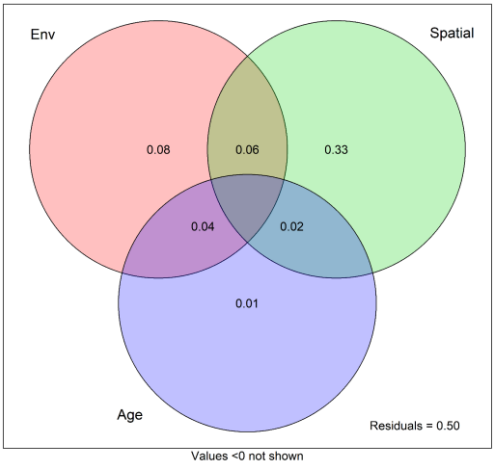

Figure 7. Venn diagram showing the variation (adjusted R^2) contributed by (1) Env: environmental factors, including topographical variables and the soil properties. (2) Spatial: PCNM factors representing the spatial structure between each pair of plots; (3) Age: Stand age of the plots.

4. Discussion

In this study, we analyzed changes in species richness and dissimilarity using multivariate analysis, and quantified the relative importance of factors regulating species turnover along a successional gradient. Our results provide insights into succession in subtropical forest, and have implications for the conservation and restoration of forest ecosystems.

4.1. Accumulation of species richness

Our results showed that in a highly degraded subtropical landscape, species accumulated mainly within the first 15-20 years of succession (Fig. 2b), a similar finding to studies in tropical forest in other areas. The rapid initial accumulation of species richness showed that a number of woody species were able to invade into grassland, although strong sunshine, high evaporation and low soil nutrient levels all pose difficulties for most tree species (Tabarelli et al., 2008). The indicator species analysis suggested that only a few species can recruit in relatively high abundance (Fig. 4) at the early stage.

Rapid accumulation of species is essential for succession, but it is also constrained by a number of factors. First, the degree of habitat degradation and past land use negatively influence the dispersal and recruitment of early successional species (Collins et al., 2017). Abiotic factors such as strong UV, seasonality of rainfall, drought, high evaporation, poor soil conditions and wind cause environmental filtering (Cadotte and Tucker, 2017) whereas biotic barriers such as invasive species and the lack of dispersal agents will limit the recruitment of suitable grassland colonisers. Second, if the local species pool is reduced, only a subset of species is available to contribute to the community assembly. This is especially true for areas with high local extinction debt caused by landscape scale land use change commonly encountered over large areas of the tropics. The species which survive need to possess functional traits that help them to overcome these difficulties. In other words, environmental filtering will be more important to the community assembly during early succession.

4.2. Divergence of Species Composition

The rapid accumulation of species richness does not mean that species composition has also recovered at a similar rate (Williamson et al., 2014). In fact, our results showed that species composition was still random and convergence to the old-growth forest could not be observed (Fig. 5 a, b). Our results also showed that species composition was not in line with the proposed framework of succession for the subtropical forests of south China (Peng, 1996; Wang and Peng, 1987). The deviation could be explained by the degree of degradation and reduced species pool. *Pinus massoniana*, for example, a key species in the regional framework of succession, used to be common in secondary vegetation throughout Hong Kong, but was eliminated by the Pinewood nematode (*Bursaphelenchus xylophilus*) during the 1960-1970s (Abbas et al., 2016; Corlett, 1999). Local extinction of this conifer

388 species inevitably altered the species composition, and therefore the species composition of
389 the proposed framework of succession could not be attained.

390 Divergence in species composition along the successional gradient has been reported by
391 other researchers (Lepš et al., 1991; Norden et al., 2011; Rolim et al., 2017).The divergence
392 of species composition suggests that plots within each age class may have taken different
393 successional pathways, especially under the different land use histories, as well as the
394 random order of arrival. In our results, the divergence of species composition likely started
395 from the mid successional stage when the sun-loving species were being excluded. A
396 possible explanation is that, as soon as the mid-successional species are colonized, they
397 became dominant due to the priority effect (Fukami, 2015). Our results showed that species
398 composition was convergent in the mid- successional stages, implying that communities
399 might have entered their own alternative stable states (Beisner et al., 2003).

400 **4.3. Indicator species for each age class**

401 If a species is more abundant in disturbed areas or in the secondary vegetation, it is
402 often considered a "pioneer" species. These species are usually adapted to exposed habitats
403 and are able to produce high numbers of smaller seeds, often dispersed by wind, birds or
404 small mammals (Zhou et al., 2017; Zhuang and Yau, 1998). Their seedlings can also
405 benefit from the exposed habitat and are often more tolerant to drought. These
406 characteristics ensure their successful colonisation and recruitment in the grassland. Once
407 colonized, these species create sheltered habitats for the mid-successional species, and the
408 modified environment may favor their recruitment. Thus, these "pioneer" species would be
409 gradually replaced by mid- or late-successional species. However, our results showed that
410 these "pioneer" species, although perhaps not occurring within the first few years of
411 succession, are able to recruit and persist in the mid successional stages or in old growth
412 forest, eg. *Aporosa octandra* and *Psychotria asiatica* (SI Table 2). We argue that the

definition of "pioneer" species may not be sufficiently accurate, and the role of a species and its habitat preferences should be assessed from various aspects. Nevertheless, the prevalence of sun-loving species suggests strong environmental filtering (Kraft et al., 2015) at the beginning of forest succession in the degraded subtropical landscape.

We did not detect species with higher indicator values for the plots within in the middle age classes, probably due to either: (1) Randomness in species occurrences, especially caused by the priority effect (Fukami, 2015) or (2) High turnover in species composition. However, the contribution of these factors still requires further exploration.

The results of betadisper (Anderson, 2006) showed that plots over 70 years were still remarkably dissimilar (Fig. 6, a,b). The number of species in the oldest ages classes is even lower than in the younger plots, indicating that species richness does not accumulate from the mid to late successional stages, and might even decline. Both a reduced species pool, and competitive exclusion (Bachelot et al., 2015) may help to explain a lower species richness and a simpler structure of the old growth forest. The divergence in species composition between the plots implied that the community structure was still far from converging to "climax" forest (Zhuang, 1997; Zhuang and Corlett, 1997).

4.4. Factors contributing to species turnover

Our analysis revealed that spatial distance and environmental variables jointly explained more than 47% of the variation, indicating a strong role of dispersal or colonisation limitation (Knappová et al., 2017), reduced species pool (Karger et al., 2015) and environmental filtering among the plots. This is consistent with the general finding that plants are dispersal limited (D'Amen et al., 2018; Jacquemyn et al., 2001; Sydenham et al., 2017)), suggesting species' order of arrival (Fukami, 2015) may be important in the maintenance of species composition. Variation partitioning in the primary forest often

suggests that environmental variables explain a higher amount of variation (Legendre et al., 2009). Our results suggest that the relative importance of forces influencing species diversity within secondary forest may differ from the forces governing diversity in primary forests. The successful establishment and expansion of late successional species does not only rely on the amount of seeds that the maternal trees can produce, but also their dispersal agents. However, as the forest becomes degraded, mammals and birds specifically relying on these forest ecosystem may become extinct in the region, and the remaining dispersal agents are often smaller in body size (Corlett, 2011; Corlett and Hau, 2000). Pioneer species are often smaller seeded, and dispersed by wind or water, but late successional species/climax species tend to have larger seeds or fruits (Holl, 2002). It is not surprising that a number of species will be unable to recruit on their own, in the absence of dispersal agents. To overcome the barriers of seed dispersal and establishment, reintroduction of dispersal agents (Ruxton and Schaefer, 2012) would be necessary where the ecosystem provides enough food and nesting places, but this requires careful consideration.

4.5. Role of Environmental Filtering and Stochastic Processes

Variation partitioning not only highlighted the role of spatial distance, but also of environmental filtering in determining species composition. Studies have shown the existence of habitat preference even at the community scale (Baldeck et al., 2013; Gunatilleke et al., 2006). Altitude, aspect, and steepness of slope all contribute to the distribution of species, and confirm the role of niche-based processes in governing species composition during succession. Almost half of the variation in species composition remains unexplained (Fig. 7). The unexplained variation is usually attributed to stochastic processes (Chase and Myers, 2011; Legendre et al., 2009; Tilman, 2004), for example, seed dispersal (Corlett and Hau, 2000), seed germination (Zhang et al., 2014) and recruitment of seedlings (Zhu et al., 2018), which are prevalent across scales. Other factors showing randomness,

462 depending on the spatial scale, include the above mentioned ecological processes, as well as
463 the environmental heterogeneity which the existing topological variables and the soil
464 properties cannot capture. Good examples are temporary streams and the
465 formation/movement of sunlight spots. Overall, our result confirm that community structure
466 is determined by both niche-based and stochastic processes (Måren et al., 2018).

467 ### 4.6. Implications for conservation action

468 Restoration efforts have been taken to overcome the barriers delaying succession, and
469 to speed up the recovery of diversity (Ghazoul and Chazdon, 2017). This is extremely
470 challenging for places where the active species pool is reduced and communities have
471 entered alternative stable states. In the absence of primary forest as reference (Brudvig et
472 al., 2017), it is even more difficult to identify species' membership or roles in a habitat.
473 Further experimental studies must be conducted to understand the mechanisms underlying
474 species assembly during succession, ideally by taking primary forest from neighboring
475 regions as templates to determine a practical approach for overcoming arrested succession
476 (Ghazoul and Chazdon, 2017).

477 ## 5. Conclusion

478 Our study confirmed that secondary vegetation is dominated by sun-loving species at
479 the early stage of succession, and the species composition becomes divergent during the
480 mid-successional stages due to randomness, environmental filtering, and dispersal
481 limitation in colonisation and recruitment of species, as showed by the indicator values
482 throughout the successional gradient. The results suggest that, in highly degraded areas,
483 secondary forest communities may follow different successional pathways and their species
484 composition may not necessarily converge. We found spatial distance played a more
485 important role than environmental distance in determining the species composition in a
486 secondary forest, reflecting a higher importance of dispersal limitation in this landscape.

We conclude that, without active restoration, the secondary forest will not progress to a diverse and healthy forest, and successful restoration of the ecosystem will require more effort and careful design.

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Author's contribution

The idea was conceived by S.A., G.F. and J.E.N., data were collected by S.A. and J.E.N., species were identified by J.Z., and data analysis was performed by J.Z and S.A. The manuscript was written by J.Z., S.A., J.E.N. and G.F.

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